

REVIEW OF *LEPTOMERYX* (ARTIODACTYLA, LEPTOMERYCIDAE)
FROM THE ORELLAN (OLIGOCENE) OF NEBRASKAWILLIAM W. KORTH^{1,2}

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ABSTRACT

Several hundred specimens were examined of the artiodactyl *Leptomeryx* from the Orellan of North America. The dental morphology used to distinguish Chadronian species of the genus were examined for consistency in the Orellan sample. Based on the consistent dental characters established, three distinct species are recognized from the Orellan: *L. evansi* Leidy, *L. exilis* Cook, and *Leptomeryx elissae* new species. Additional material of *Leptomeryx* from the Whitneyan was also examined and suggests that *L. minimus* Frick and *L. lenis* Cook may be junior synonyms of *L. exilis* and *L. evansi*, respectively.

Two distinct lineages of *Leptomeryx* are recognized that range from the Chadronian through the Whitneyan and possibly Arikareean, the *L. yoderi*-*L. mammifer*-*L. exilis*-*L. obliquidens* lineage and the *L. speciosus*-*L. evansi* lineage. It is likely that the Arikareean leptomerycid *Pronodens* Koerner is derived directly from the *L. evansi* lineage.

KEY WORDS: *Leptomeryx*, Chadronian, Orellan, Oligocene, Artiodactyla

INTRODUCTION

Historical Review

Leidy (1853) first named *Leptomeryx evansi* as a new genus and species from what is now known to be the Orellan Brule Formation in South Dakota. Since that time, 16 species of *Leptomeryx* have been named, ranging in age from Duchesnean to Hemingfordian (Cope, 1886, 1889; Douglass, 1903; Lambe, 1908; Lull, 1922; Cook, 1934; Frick, 1937; Wilson, 1974). The majority of these species were Chadronian in age (see Webb, 1998 for review). The only Orellan species named, other than the type species, was *L. exilis* from Sioux County, Nebraska (Cook, 1934). In his review of the White River artiodactyls, Scott (1940) cited only a single species from the Orellan, the type species, *L. evansi*.

Heaton and Emry (1996) reviewed the Chadronian species of *Leptomeryx* and followed Scott (1940) in concluding that there was only a single species of leptomerycid from the Orellan, *L. evansi*, and that the other nominal species from the Orellan were merely synonyms of *L. evansi*. Galbreath (1953) recognized only *L. evansi* in his Orellan fauna from northeastern Colorado, but cited a single specimen as *Leptomeryx* sp. The latter specimen was a maxillary fragment with upper cheek teeth that were smaller than referred specimens of upper dentitions of *L. evansi*. In the most recent review of the Leptomerycidae, Webb (1998) also agreed that only a single species of *Leptomeryx* existed in the Orellan and sug-

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gested several synonymies for the known Chadronian to Arikareean species of *Leptomeryx*.

Black (1978) named a new Duchesnean genus of leptomerycid, *Hendryomeryx*. He distinguished *Hendryomeryx* from *Leptomeryx* by its more primitive, lower crowned cheek teeth. He referred a species previously identified as *Leptomeryx* to it, *H. defordi*, from Texas (Wilson, 1974). Storer (1981) also referred one of Cope's Chadronian species, *L. esulcatus*, to *Hendryomeryx*. Webb (1998:fig. 31.6) listed *Hendryomeryx* from the Orellan of Montana without a citation and figured *Hendryomeryx* as surviving into the Whitneyan. However, several authors have considered *Hendryomeryx* as a junior synonym of *Leptomeryx* (Heaton and Emry, 1996; McKenna and Bell, 1997).

In all, as many as three species of leptomerycid or as few as one species may be present in the Orellan of North America. No review of Orellan *Leptomeryx* has ever been made at the species level. With the large samples of *Leptomeryx* now available, such a study is warranted.

Fossil Material

Extensive collections of Orellan *Leptomeryx* are available in several institutions in North America. The bulk of the material studied was from the Orella Member of the Brule Formation, Sioux County, Nebraska. However, comparative samples from the Orellan of North Dakota, South Dakota, Colorado and Wyoming were also studied (see Appendices 1 and 2). The institutions providing the sample were as follows: American Museum of Natural History (AMNH), Carnegie Museum of Natural History (CM), National Museum of Natural History, Smithsonian (USNM), University of Nebraska State Museum (UNSM) and Yale-Peabody Museum (YPM). Many of these samples were collected as early as the early 1900s and no distinction was made as to horizon other than "Oreodon beds" or "Lower Brule" (=Orella Member, Brule Formation). A large, stratigraphically controlled sample was available from the UNSM. The stratigraphic divisions of this sample were based on the divisions of the Orella Member defined by Schultz and Stout (1955): Orella A, Orella B, Orella C, and Orella D (from lowest to highest). A smaller stratigraphically controlled sample from the White River Formation of Niobrara County, Wyoming, from AMNH was also included in this study. Small samples of Whitneyan *Leptomeryx* from the collections of the AMNH and UNSM were also examined and measured for comparison.

Methods

Morphology.—Heaton and Emry (1996) used several features of the lower cheek teeth to distinguish the Chadronian species of *Leptomeryx*. Each of these is explained below and was identified on the Orellan sample of *Leptomeryx* in an attempt to establish its usefulness in separating species (Fig. 1).

1) entoconulid on M_3 —The posterolingual cusp on the talonid of M_3 (entoconulid) is a cylindrical cusp with a deep valley posterior to it, separating it from the hypoconulid on specimens of *L. speciosus* and *L. evansi* (abbreviated S/E). The entoconulid on these teeth is also subequal in height to the hypoconulid. On specimens of *L. yoderi* and *L. mammifer* this cusp is more conical (triangular in lingual view) and slopes more gently posteriorly, eliminating the deep valley between it and the hypoconulid (Y/M). The entoconulid on these teeth is lower in height than the hypoconulid.

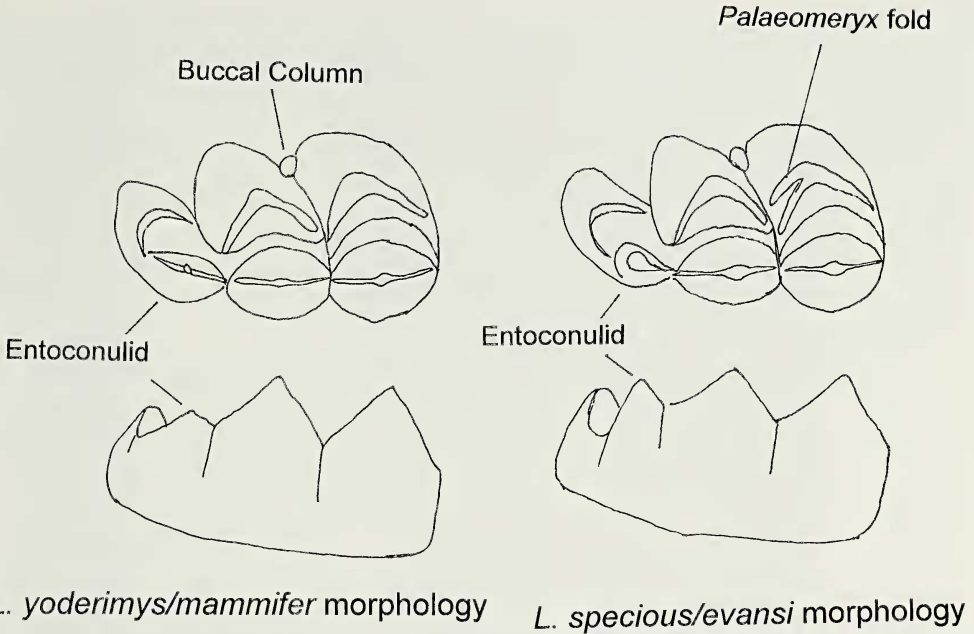


Fig. 1—Schematic diagrams of left M_3 of *Leptomeryx* (occlusal view above, lingual view below) indicating features discussed in text and variation of morphology of entoconulid. Modified from Heaton and Emry (1996:fig. 9).

2) *Palaeomeryx* fold—A small loph that originates from the protoconid on the lower molars and runs down the posterior slope of that cusp is lacking in Chadronian species of *Leptomeryx* but is present on *L. evansi*.

3) enamel wrinkling—Primitively, the enamel of the cheek teeth is smooth as in the Chadronian species of *Leptomeryx*; however, in *L. evansi* it is highly rugose.

4) position of protoconid loph on P_3 —Heaton and Emry (1996) found the major loph running posteriorly from the apex of the protoconid on P_3 (although highly variable) generally ran along the lingual side of the tooth in Chadronian species, but along the buccal edge of the tooth in *L. evansi*.

5) buccal column—The styler cusp between the buccal cusps of the lower molars, if present, is usually a tall column. Its height and presence is variable.

Measurements.—Size has been shown to distinguish species of *Leptomeryx* with similar dental morphology (Heaton and Emry, 1996). Measurements of all cheek teeth of the specimens examined in this study were taken. Maximum widths and lengths of each tooth and alveolar lengths of the molar tooth rows were taken on all specimens. All measurements were taken to the nearest 0.1 mm.

RESULTS

Characters Used to Distinguish Species

Of the characters observed, the most reliable is the morphology of the entoconulid on the talonid of M_3 . The difference between the *L. evansi*/*L. speciosus* morphology and the *L. yoderi*/*L. mammifer* morphology (Heaton and Emry, 1996: fig. 9) is consistently distinguishable. In addition to the differences in the entoconulid cited and figured by Heaton and Emry (1996), it is also evident that in

the Y/M morphology the cusp is lower than both the hypoconulid and the entoconid and does not show signs of wear until the latter two cusps are moderately worn. In specimens with the S/E morphology, the entoconulid is as tall as the adjacent cusps.

The presence of the *Palaeomeryx*-fold on the lower molars is fairly consistent. The *Palaeomeryx*-fold is absent from all specimens with the Y/M entoconulid morphology. Specimens referred to *Leptomeryx evansi* nearly always have this feature present, but there is some variability. In specimens of *Leptomeryx evansi* containing all of the molars, this feature is present on all M₁s, 90% of the M₂s, and 83% of the M₃s. Therefore, the absence of this character was less diagnostic on isolated M₃s.

The degree of enamel crenulation on the molars is generally consistent between the recognized species of *Leptomeryx*, but the range of variability has nearly a complete overlap. The amount of crenulation of the enamel was subjectively recorded numerically from 0 (smooth enamel) to 2 (most crenulated) in increments of 0.5. Specimens of *L. evansi* ranged from 0.5 to 2.0, with a mean of 1.5, meaning that the teeth were generally fairly strongly wrinkled. The specimens with the Y/M entoconulid were generally much smoother, ranging from 0 to 1.5 with a mean of 0.5. It is evident, looking at a large population, that there is a general trend for more highly wrinkled enamel in *L. evansi*, but the overlap is quite large and could not easily be applied to a very small sample of specimens. Similar results were found with the upper cheek teeth as well.

As indicated in Tables 1–4, the teeth of these species differ in size. With approximately 40% overlap, however, large samples with good provenience are needed to distinguish species. Lower dentitions referred to *L. evansi* were generally larger than those with the Y/M entoconulid. Similar results were found with the upper dentitions.

The remainder of the characters analyzed by Heaton and Emry (1996) for the lower dentitions did not appear to be consistent enough to separate species of *Leptomeryx*. For example, presence and size of buccal column on lower molars and posterior protoconid loph on P₃ were extremely variable. The posterior lophid from the protoconid on P₃ of all specimens was directed along the buccal side of the tooth; none of the Orellan specimens has this lophid on the lingual side of the tooth. The buccal column is present on nearly all the specimens from the Orellan and is highly variable in size, ranging from a small cuspule to a distinct column. No general trend in this morphology can be used to separate the Orellan species of *Leptomeryx*.

No features of the upper cheek teeth were examined by Heaton and Emry (1996). However, in the present study there are two features of the upper dentition that appear distinguishable between species. First is the amount of enamel wrinkling, which is reflective of this character in the lower dentition, and the second is the development of a mid-lingual column (protostyle). This cusp is generally large and columnar on most specimens, but is entirely lacking in others. Species are also separable on size of the upper dentitions as noted above. In general, the upper molars of the smaller species are also distinguishable from those of *L. evansi* by their proportions. In *L. evansi*, the upper molars are nearly square (width equal to length), whereas in the smaller species, the upper molars are generally wider than long except M³ (Tables 1 and 4).

There appear to be differences between species based on morphology of the mandible, but the features are known only on a few specimens, so their consis-

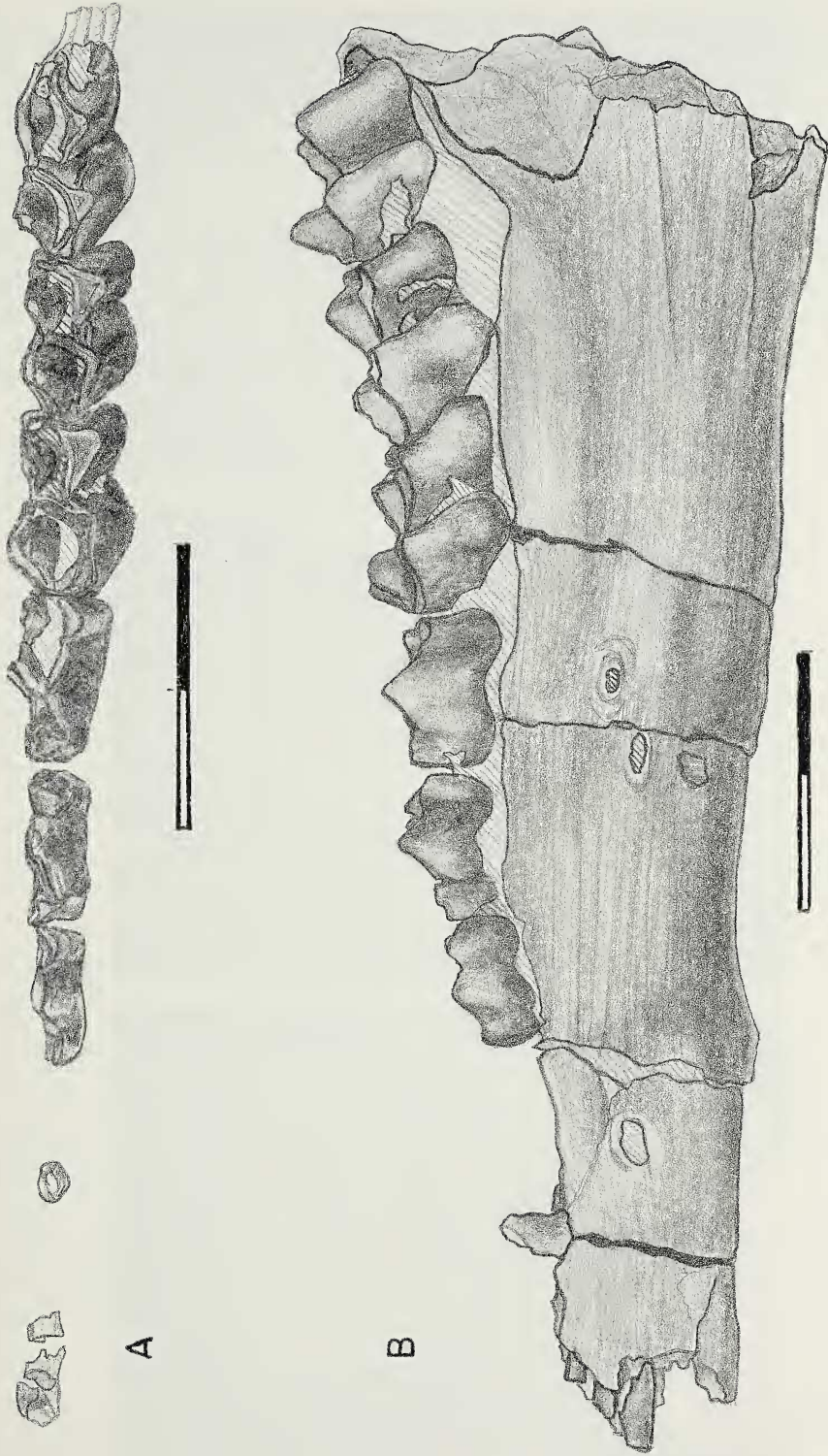


Fig. 2—Mandible and lower cheek teeth of *Leptomeryx evansi*, CM 512A. A. Occlusal view, P₁-M₃. B. Lateral view of mandible. Bar scale = 1 cm.



tency is not known. On mandibles of *Leptomeryx evansi* (Fig. 2) there are one or more accessory mental foramina. They are always below P_4 . This is also true of an intermediate-sized species with the *L. evansi*-type of M_3 morphology (described below). In the known mandibles of the smallest species, there are also accessory mental foramina. One is always ventral to P_3 , and if there is more than one, the second is below P_4 (Fig. 6), as in *L. evansi*.

Another mandibular difference is in the position of P_1 . In all species of *Leptomeryx* there is a diastema between P_1 and P_2 . The main mental foramen is below this diastema. In *L. evansi* P_1 is dorsal to the anterior margin of the mental foramen (Fig. 2). In the smallest species, the alveolus for P_1 is 2.4 mm anterior to the mental foramen. Because of the low number of complete mandibles in the fossil sample, these differences are not included in the diagnoses of the species listed below.

Species Recognized

Three species of *Leptomeryx* can be recognized from the Orellan of Nebraska and the northern Great Plains. *Leptomeryx evansi*, the type species of the genus, is separable from the other species by its larger size, more highly crenulated enamel on the cheek teeth, presence of a protostyle on the upper molars, and S/E morphology of the entoconulid on M_3 .

A second species with the S/E-type of entoconulid morphology of M_3 is also recognizable. It is generally smaller than *L. evansi* with less wrinkling of the enamel and lacks the *Palaeomeryx*-fold on the lower molars.

The third species is the smallest. It lacks a protostyle on the upper molars, has less crenulated enamel on the cheek teeth, has the Y/M morphology of the entoconulid, and lacks a *Palaeomeryx*-fold on the lower molars.

SYSTEMATIC PALEONTOLOGY

Leptomeryx Leidy, 1853

Leptomeryx evansi Leidy, 1853

(Fig. 2, 3; Tables 1 and 2)

Type Specimen.—USNM 157, partial skull and associated mandible.

Referred Specimens.—See Appendix 1.

Horizon and Locality.—Holotype from Orellan White River Group, South Dakota. Referred specimens from the Orellan of the northern Great Plains.

Emended Diagnosis.—Intermediate-sized species; enamel on cheek teeth highly crenulated; *Palaeomeryx*-fold present on lower molars; entoconulid on M_3 cylindrical with deep posterior valley, separating it from the hypoconulid; protostyle present on upper molars.

Discussion.—*Leptomeryx evansi* is, by far, the most common of any of the Orellan species of the genus, outnumbering the other species as much as 50 to 1 in some collections. This species shows little variation throughout its chronological and geographic range. There is virtually no difference in size of the samples

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Fig. 3—Cheek teeth of *Leptomeryx evansi*. A. Occlusal (above) and lingual view of M_1 – M_3 , CM 175. B. Occlusal view of M^1 – M^3 , UNSM 119726. Bar scale = 1 cm.

Table 1.—Dental measurements of *Leptomeryx evansi* from the Orellan (all horizons and localities combined). Abbreviations: L, length; W, width; N, number of specimens; M, mean; OR, observed range of size; sd, standard deviation; CV, coefficient of variation. All measurements in mm.

	M ₁ -M ₃	LM ₁	WM ₁	LM ₂	WM ₂	LM ₃	WM ₃
N	53	51	48	80	79	129	128
M	22.0	6.2	4.5	6.6	4.9	9.3	4.7
OR	19.8-24.2	5.3-7.2	3.8-5.2	4.2-7.5	4.1-5.4	8.0-10.7	3.7-5.5
sd	1.1	0.4	0.3	0.5	0.3	0.6	0.3
CV	5.0	6.5	6.0	7.5	6.0	6.4	7.1
	M ¹ -M ³	LM ¹	WM ¹	LM ²	WM ²	LM ³	WM ³
N	24	66	66	60	59	41	41
M	19.0	6.3	6.3	6.7	6.8	6.7	6.4
OR	17.8-20.6	5.4-7.0	5.1-7.5	5.8-7.5	5.2-8.4	6.0-7.7	5.4-7.6
sd	0.8	0.3	0.5	0.4	0.7	0.4	0.6
CV	4.2	5.2	8.1	5.4	9.9	6.1	8.8

from Orella A through Orella D (Table 2). Geographically, the only sample that shows any variation is that from Wyoming. The Wyoming sample of *L. evansi* has a slightly longer M₃ than all of the other samples. However, the overlap of the size ranges with other samples is nearly 100% and the difference in the mean is less than 10% of the length of the tooth. This larger size of M₃ is also reflected in the measurement of the molar row (M₁-M₃). Heaton and Emry (1996) also measured a sample from the lower part of the Orellan in Wyoming and produced measurements similar to those of our sample, slightly larger than the remainder of the samples. This is not viewed as enough difference to suggest a separate species with the Wyoming material, only a slight geographic variation in the Wyoming population.

Leptomeryx elissae, new species

(Fig. 4, 5; Table 3)

Type Specimen.—UNSM 119638, mandible with left P₃-M₃.

Referred Specimens.—CM 73416; UNSM 119636, 119637, 119639, 119640; AMNH 53626A, 606-25868, 606-25873 (all mandibles with cheek teeth).

Horizon and Locality.—Holotype from UNSM locality Sx-8, Orella Member (Orella C), Brule Formation, Sioux County, Nebraska. All referred specimens from the Orella Member (Orella C and D), Brule Formation, Sioux County, Nebraska (Orellan).

Diagnosis.—Smaller than *L. evansi*; enamel of cheek teeth smooth (less crenulated than in *L. evansi*); S/E-type of entoconulid on M₃; *Palaeomeryx*-fold lacking on lower cheek teeth.

Etymology.—Named for a daughter of one of the authors (MED).

Discussion.—A small group of specimens that share the S/E-type of entoconulid on M₃ with *Leptomeryx evansi* are distinguishable from the latter by their slightly smaller size, less crenulated enamel on the molars, and lack of a *Palaeomeryx*-fold on the lower molars. This species is intermediate in size between the two other Orellan species of *Leptomeryx* (Table 3), and slightly closer to the smaller species. However, the amount of overlap in the size range with *L. evansi* is large, nearly 50%. The average amount of wrinkling on the molars is 0.7, more

Table 2.—Dental measurements of lower molars of Orellan *Leptomeryx evansi* separated stratigraphically and geographically. Abbreviations as in Table 1.

	M ₁ –M ₃	LM ₁	WM ₁	LM ₂	WM ₂	LM ₃	WM ₃
Nebraska (all levels)							
N	41	39	38	66	65	112	112
M	21.8	6.2	4.5	6.6	4.9	9.2	4.7
OR	19.8–24.2	5.3–7.0	3.8–4.9	4.2–7.5	4.1–5.4	8.0–10.7	3.7–5.5
sd	1.0	0.4	0.2	0.5	0.3	0.6	0.3
CV	4.8	6.5	5.5	7.8	6.1	6.3	6.9
Nebraska (Orella A)							
N	1	1	1	3	3	14	14
M	20.8	5.7	3.8	6.4	4.4	9.0	4.6
OR	—	—	—	6.0–6.9	4.1–4.7	8.1–9.6	3.7–5.3
sd	—	—	—	0.5	0.3	0.4	0.5
CV	—	—	—	7.0	7.0	4.7	10.1
Nebraska (Orella C)							
N	3	3	3	6	6	15	15
M	21.7	6.2	4.4	6.8	4.9	9.0	4.7
OR	20.5–22.5	6.1–6.4	4.1–4.6	6.4–7.2	4.4–5.1	8.1–9.9	4.1–5.2
sd	1.1	0.2	0.3	0.4	0.3	0.6	0.3
CV	5.0	2.5	6.0	5.3	5.6	6.2	6.4
Nebraska (Orella D)							
N	—	—	—	2	2	10	10
M	—	—	—	6.7	4.5	9.2	4.6
OR	—	—	—	6.5–6.8	4.2–4.7	8.1–9.9	4.4–5.2
sd	—	—	—	—	—	0.5	0.2
CV	—	—	—	—	—	5.5	5.1
North Dakota							
N	4	4	4	5	5	7	7
M	21.7	6.1	4.5	6.5	4.8	9.3	4.6
OR	20.7–23.7	5.7–6.4	4.0–5.2	6.2–6.9	4.4–5.3	8.5–10.6	4.1–5.3
sd	1.4	0.3	0.6	0.3	0.4	0.8	0.5
CV	6.4	4.9	12.4	4.2	7.7	8.1	10.4
Wyoming							
N	7	7	5	8	8	8	7
M	22.8	6.4	4.4	6.9	5.0	9.7	4.7
OR	21.6–24.2	5.8–7.2	4.1–4.6	6.5–7.4	4.6–5.4	9.0–10.1	4.6–5.4
sd	1.1	0.4	0.2	0.4	0.2	0.4	0.2
CV	4.6	6.9	4.4	5.2	4.9	4.5	5.0

than the smaller species, less than in *L. evansi*, but with a range of from 0 to 1, less than in the smaller species (0 to 1.5).

Leptomeryx exilis Cook, 1934

(Fig. 6, 7, 8; Table 4)

Type Specimen.—AMNH 81012, partial right mandible with M₂–M₃.

Referred Specimens.—See Appendix 2.

Horizon and Locality.—Holotype from “the Brule (Middle Oligocene) beds about two miles north of Chadron, Nebraska” (Cook, 1934:154). Referred material from Orellan of the White River Group, northern Great Plains.



Fig. 4—Occlusal (above) and lingual view of M_1 – M_3 of *Leptomeryx elissae*, UNSM 119638 (holotype). Bar scale = 1 cm.

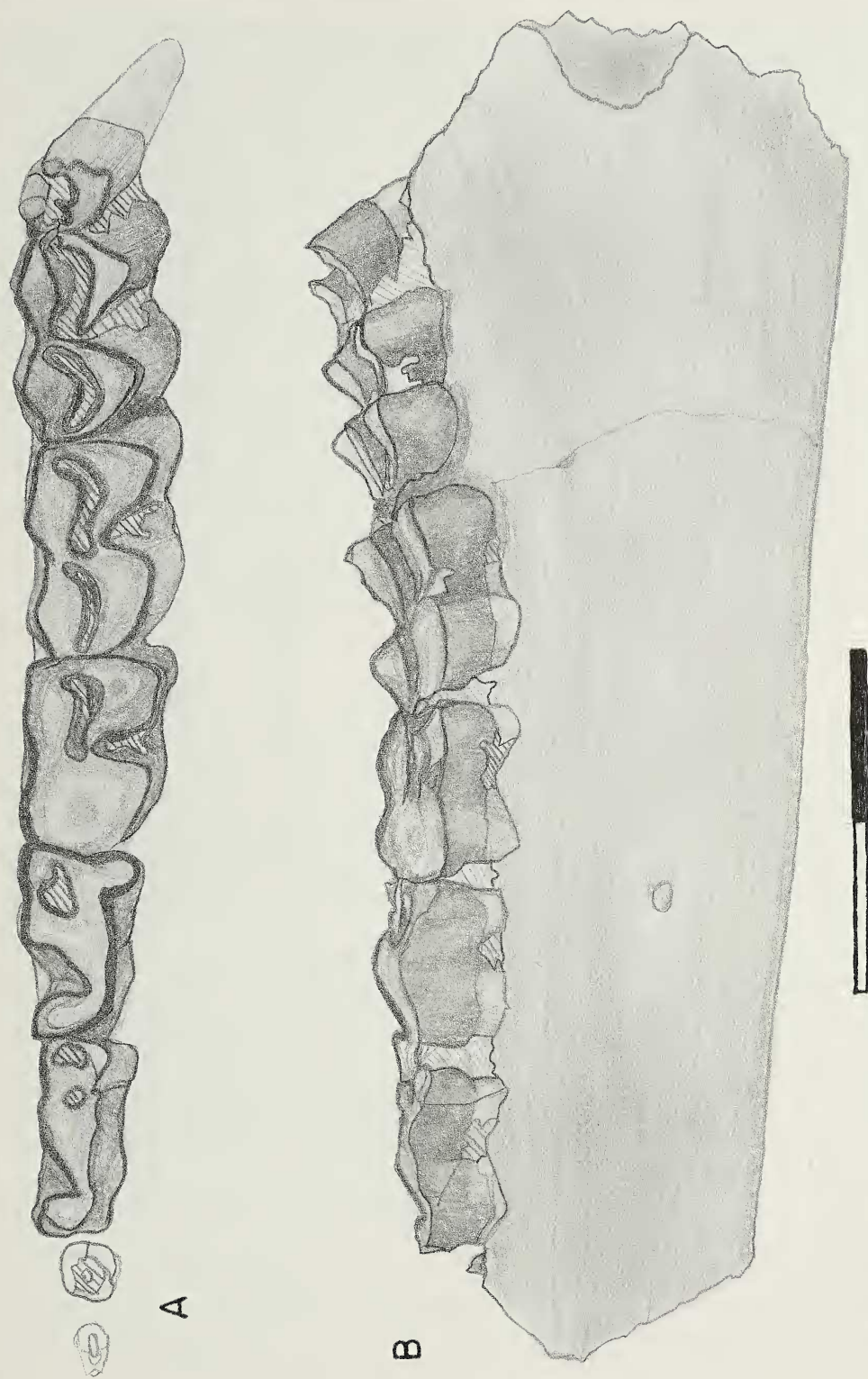


Fig. 5—Mandible and lower cheek teeth of *Leptomeryx elissae*, CM 73416. A. Occlusal view, P₃–M₃ (alveolus for P₂). B. Lateral view of mandible. Bar scale = 1 cm.

Table 3.—Dental measurements of *Orellan Leptomeryx elissae*. Abbreviations as in Table 1.

	M ₁ -M ₃	LM ₁	WM ₁	LM ₂	WM ₂	LM ₃	WM ₃
N	4	3	3	5	5	6	6
M	19.8	5.6	4.3	6.4	4.6	8.6	4.4
OR	19.4-20.4	5.1-6.0	4.0-4.6	6.0-6.7	4.4-4.9	8.0-9.2	4.2-4.6
sd	0.5	0.5	0.3	0.3	0.2	0.4	0.1
CV	2.6	8.4	7.0	4.3	4.6	4.5	3.4

Emended Diagnosis.—Smallest species of the genus; cheek teeth with little or no wrinkling of the enamel; *Palaeomeryx*-fold lacking on lower molars; Y/M type of morphology of entoconulid on M₃; upper molars wider than long (subequal in dimensions in *L. evansi*) and lacking a protostyle.

Discussion.—Specimens of *Leptomeryx exilis* are easily distinguishable from those of the other Orellan species by their smaller size and construction of the entoconulid on M₃ (Y/M-type). This species differs from *L. evansi* in lacking crenulations on the enamel of the molars, and lacking a *Palaeomeryx*-fold on the lower molars. Specimens referred to *Leptomeryx elissae* also have the S/E-type of entoconulid on M₃. The upper molars are proportioned slightly differently from those of *L. evansi* and lack a protostyle.

There appears to be no difference in size or morphology between samples of *L. exilis* from the various horizons within the Orella Member in Nebraska.

CONCLUSIONS

Orellan Leptomeryx

Contrary to recent authors (Heaton and Emry, 1996; Webb, 1998), three distinct species of *Leptomeryx* are recognizable from the Orellan of the Great Plains: *L. evansi*, *L. exilis* and *Leptomeryx elissae*. They are easily distinguishable by size and morphology of the lower third molar. All of the species of *Leptomeryx* from the Orellan are markedly smaller than the species reported from the Chadronian (see Heaton and Emry, 1996). The Chadronian species also lack crenulations of the enamel on the cheek teeth and the *Palaeomeryx*-fold found on Orellan *L. evansi*.

Heaton and Emry (1996) recognized two lineages of *Leptomeryx* in the Chadronian based predominantly on the morphology of the lower molars. One lineage consisted of *L. mammifer* and *L. yoderi* that were relatively large species with the primitive, conical entoconulid on M₃ (Y/M-type). The other lineage consisted only of *L. speciosus* in the Chadronian that was distinguished from the other species by the columnar entoconulid on M₃ (S/E-type) and slightly different size. Heaton and Emry (1996) viewed the *L. mammifer*-*L. yoderi* lineage as ending in the Chadronian, whereas the lineage represented by *L. speciosus* continued into the Orellan with *L. evansi*.

The recognition of three Orellan species demonstrates that the radiation of *Leptomeryx* in the Orellan is not as simple as previously believed. The morphology of M₃ of Orellan *L. exilis* is the same as in *L. yoderi* and *L. mammifer*, making it a likely member of the same lineage, and thus extending this lineage into the Orellan. *Leptomeryx exilis* differs from the former Chadronian species only in its much smaller size. *L. exilis* could easily be derived from late Chadronian *L. mammifer* simply by reducing its size. There appears to be no mor-

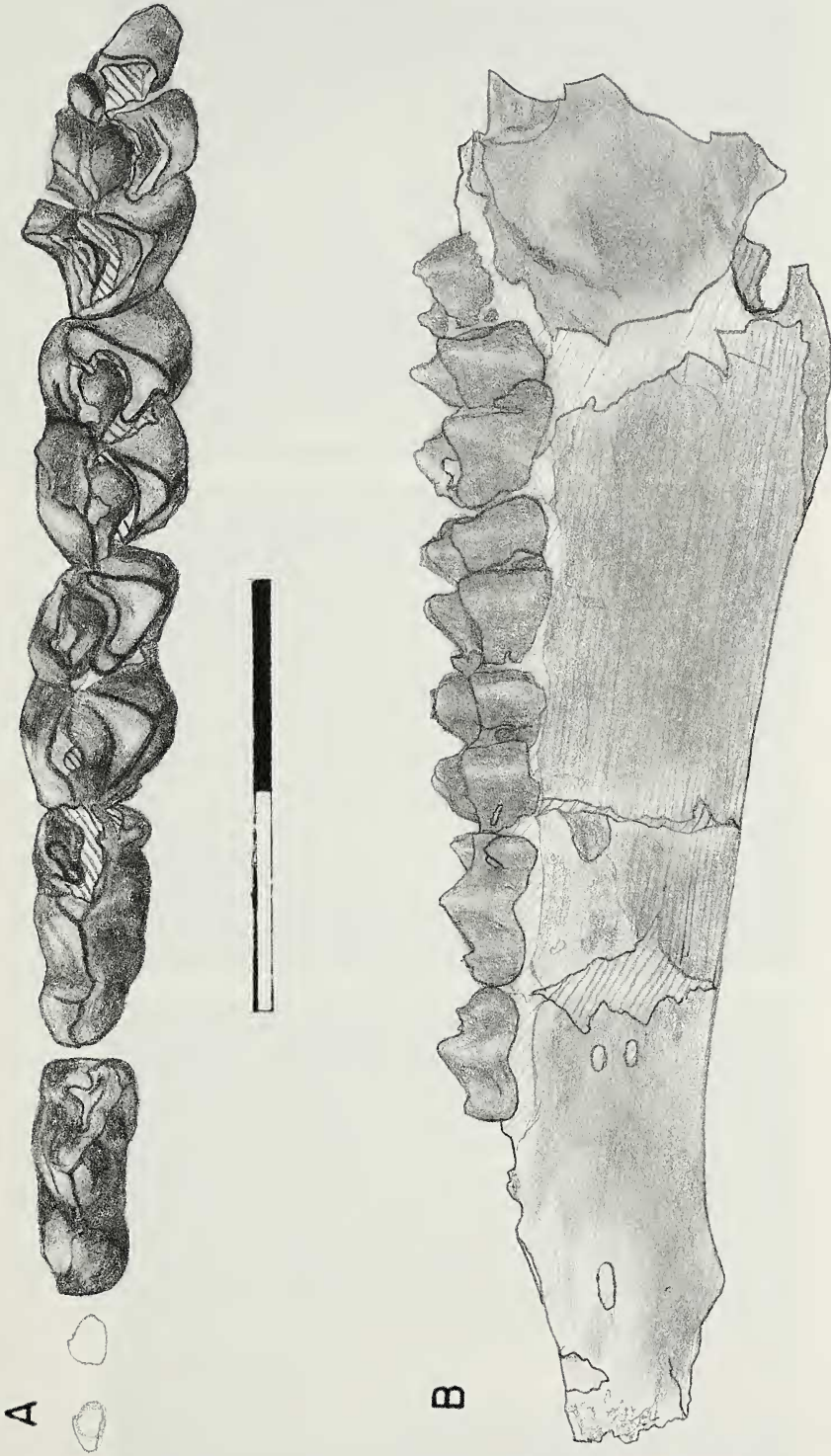


Fig. 6—Mandible and lower cheek teeth of *Leptomeryx exilis*, CM 9109. A. Occlusal view, P₃–M₃ (alveolus for P₂). B. Lateral view of mandible (alveolus for P₁). Bar scale = 1 cm.



phology that would bar *L. mammifer* from an ancestral position with respect to *L. exilis*.

Heaton and Emry (1996) viewed the Chadronian *L. speciosus* as ancestral to the Orellan *L. evansi*, the latter differing in its smaller size, more crenulate enamel on the molars, and presence of a *Palaeomeryx*-fold on the lower molars. The only difference suggested here in this *L. speciosus*–*L. evansi* lineage proposed by Heaton and Emry is the addition of another species from the Orellan. Specimens referred here to *Leptomeryx elissae* are closer to the Chadronian *L. speciosus* in morphology than to Orellan *L. evansi*, lacking the crenulations and *Palaeomeryx*-fold of the latter (primitive characters shared with *L. speciosus*). *Leptomeryx elissae* is even smaller than *L. evansi*, and thus easily distinguishable from *L. speciosus*. It appears that this lineage, characterized by the S/E-type of entoconulid on M₃, splits in the Orellan into a smaller species with simpler cheek tooth morphology (*Leptomeryx elissae*) and a larger species with more complex cheek tooth morphology (*L. evansi*). As with the other lineage of *Leptomeryx*, it is quite likely that the Chadronian *L. speciosus* is ancestral to both of the Orellan species of the genus recognized here.

Whitneyan *Leptomeryx*

Several species of *Leptomeryx* have been named from the Whitneyan: *L. lenis* Cook (1934), *L. minimus* Frick (1937), and *L. obliquidens* Lull (1922). Small samples of Whitneyan *Leptomeryx* are present in the collections of the AMNH, mainly from South Dakota, and were compared to the holotypes of these species.

The holotype of *L. lenis* (AMNH 87013) contains both upper and lower dental elements. The cheek teeth of *L. lenis* are highly crenulated, have distinct *Palaeomeryx*-folds on the lower molars and have the S/E-type of entoconulid on M₃. They are also within the size range of *L. evansi*. The holotype of *L. lenis* is indistinguishable from specimens of the Orellan *L. evansi*. Several specimens of similar size and morphology from the Whitneyan were present in the AMNH collections, and likewise, could not be separated from the Orellan samples of *L. evansi*. It appears likely that *L. lenis* is a junior synonym of *L. evansi*. This synonymy would extend the known record of *L. evansi* into the Whitneyan.

Among the Whitneyan specimens present in the AMNH collections are several that are similar to *L. evansi* in morphology (Fig. 9), but are beyond its range of size (both smaller and larger). These specimens may well represent additional species of *Leptomeryx* from this horizon.

The holotype (AMNH 1347a) and paratype (AMNH 1347) of *L. minimus* from the Whitneyan of South Dakota are small in size, have the Y/M-type of M₃, lack crenulations on the cheek teeth, and lack the *Palaeomeryx*-fold on the lower molars (Fig. 10). In size and morphology, these specimens do not differ from those referred to *L. exilis* from the Orellan. The additional Whitneyan specimens of similar size and morphology in the AMNH collections are also indistinguishable from those of *L. exilis* (Fig. 11). As with *L. evansi* and *L. lenis*, it appears that *L. minimus* is a junior synonym of *L. exilis*, thus extending the record of the latter from the Orellan into the Whitneyan.

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Fig. 7—Cheek teeth of *Leptomeryx exilis*. A. Occlusal (above) and lingual view of M₂–M₃, AMNH 81012 (holotype). B. Occlusal view, P³–M³, CM 73412. Bar scale = 1 cm.

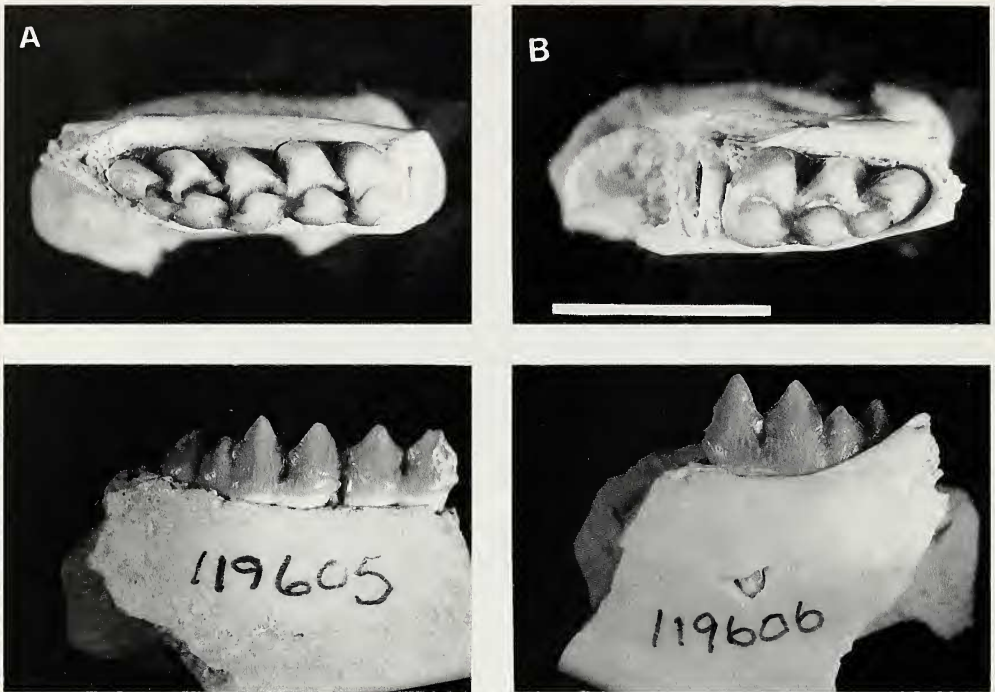


Fig. 8—Occlusal (above) and lingual views of M_3 s of *Leptomeryx exilis*. A. UNSM 11605. B. UNSM 119606. Bar scale = 1 cm.

Leptomeryx obliquidens was also described from the Whitneyan of South Dakota (Lull, 1922). It is much larger than any of the other species of the genus, nearly twice the size of *L. exilis*. It is known only from the holotype (YPM 10541) and one referred specimen (YPM 2248). It has a unique combination of morphologies. The lower molars lack the *Palaeomeryx*-fold and have the Y/M-type of entoconulid on M_3 (as in *L. exilis*), but the cheek teeth are highly crenulated, as in *L. evansi* (Fig. 12). The upper molars, although heavily worn, show no signs of a protostyle. No additional specimens referable to this species could be found

Table 4.—Dental measurements of Orellan *Leptomeryx exilis*. Abbreviations as in Table 1.

	M_1-M_3	LM_1	WM_1	LM_2	WM_2	LM_3	WM_3
N	19	17	17	41	40	68	68
M	19.8	5.4	4.1	6.0	4.5	8.3	4.4
OR	18.0–21.0	4.8–5.8	3.6–4.5	5.1–7.0	3.9–5.2	6.7–9.3	3.4–5.3
sd	0.7	0.3	0.2	0.4	0.3	0.5	0.4
CV	3.7	4.8	6.0	6.4	7.1	6.3	8.0
	M^1-M^3	LM^1	WM^1	LM^2	WM^2	LM^3	WM^3
N	3	4	4	5	5	4	4
M	16.9	5.7	6.0	6.0	6.5	6.1	6.1
OR	16.6–17.2	5.4–5.9	5.8–6.4	5.9–6.2	5.9–7.1	5.9–6.4	5.4–6.5
sd	0.3	0.3	0.3	0.1	0.5	0.2	0.5
CV	1.8	3.9	4.5	2.0	7.3	3.6	7.9

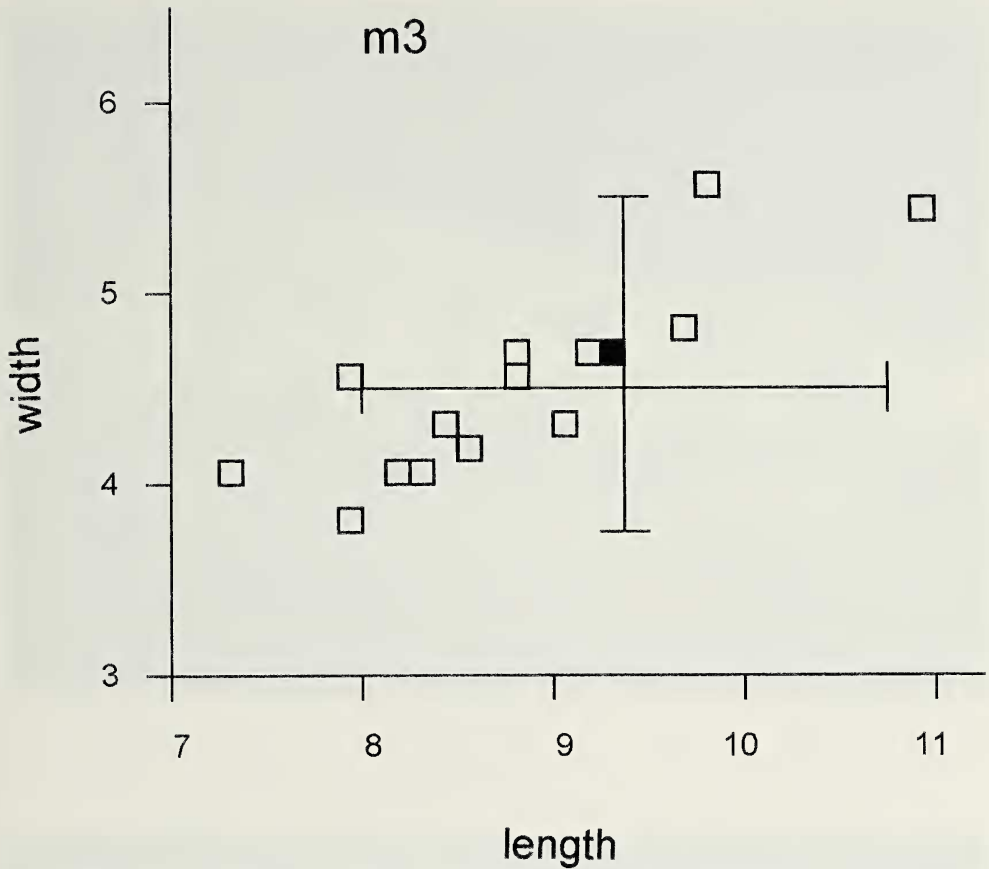


Fig. 9—Scatter diagram of length vs. width of M_3 of *Leptomyerx evansi*-like specimens (S/E-type entoconulid) from the Whitneyan. Crossed lines indicate range of size of Orellan *L. evansi*. Darkened square represents holotype of *L. lenis* (AMNH 81013). Scales in mm.

in any collections. It appears most likely that *L. obliquidens* is part of the *L. yoderi*–*L. mammifer*–*L. exilis* lineage, but that it has attained crenulated molars separately from those of *L. evansi*.

Arikareean Leptomeryx

Although several isolated and fragmentary specimens of *Leptomeryx* have been reported from the Arikareean (see Webb, 1998:471), only a few species have been named. Douglass (1903) named *L. transmontanus* from Montana. However, in an unpublished dissertation, Rasmussen (1977) demonstrated that this species was referable to the more derived genus of leptomerycid, *Pronodens* Koerner, 1940 (also see Taylor and Webb, 1976).

The only other Arikareean species referred to *Leptomeryx* is *L. agatensis* from Sioux County, Nebraska (Cook, 1934). This species is known only from the holotype, a maxilla with upper cheek teeth (AMNH 81505). In size and morphology, this specimen is not separable from upper dentitions of *L. evansi*. Due to the poor record of this species it is impossible at present to recommend the synonymy of



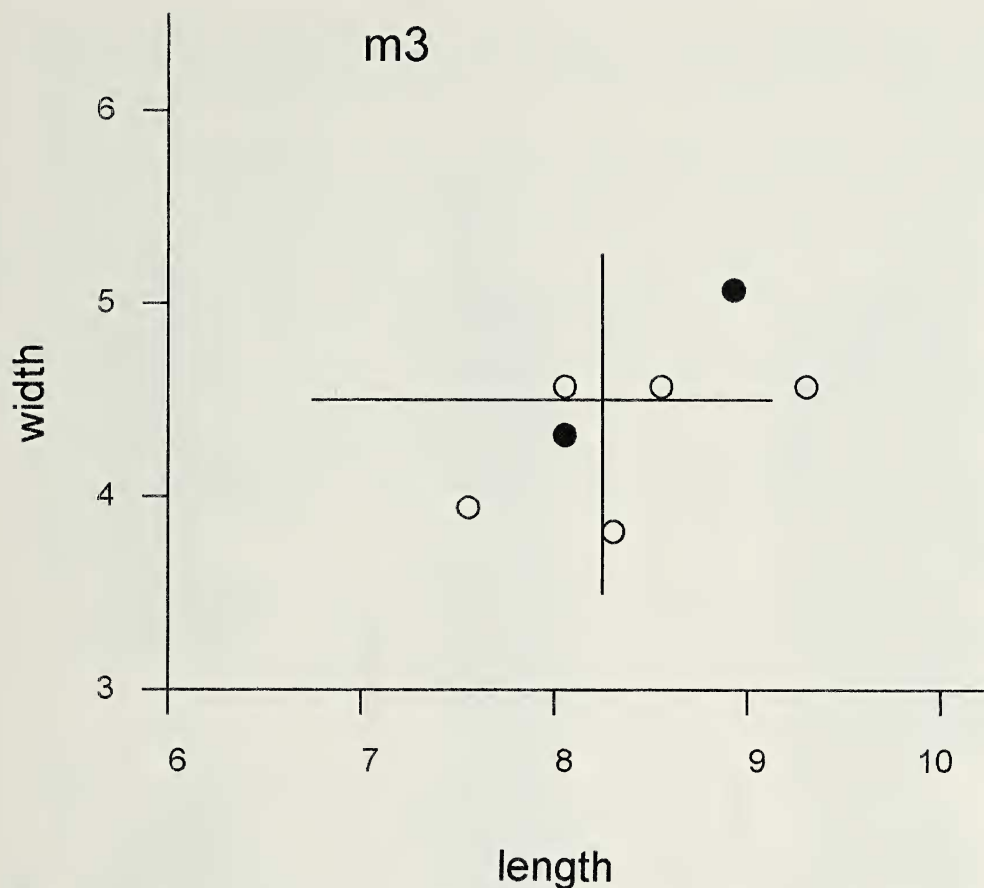


Fig. 11—Scatter diagram of length vs. width of M_3 of *Leptomeryx exilis*-like specimens (Y/M-type entoconulid) from the Whitneyan. Crossed lines indicate range of size of Orellan *L. exilis*. Darkened circles represent holotype and paratype of *L. minimus* (AMNH 1347a and AMNH 1347). Scales in mm.

these two species. It is equally as likely that *L. agatensis* is referable to a species of the Arikareean leptomerycid *Pronodens*, the latter differing from *Leptomeryx* mainly in the morphology of the anterior dentition which is not preserved in the holotype of *L. agatensis*. Webb (1998) listed *L. agatensis* as a synonym of *L. obliquidens*. The marked difference in size of these species makes it very unlikely that they are synonyms.

Relationships of North American Leptomeryx

Two distinct lineages of *Leptomeryx* can be recognized from the Chadronian to the Whitneyan of North America. One contains the Chadronian species *L. yoderi* and *L. mammifer*; the Orellan species *L. exilis*, and the Whitneyan *L.*

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Fig. 10—Occlusal (above) and lingual views of M_1 – M_3 *Leptomeryx minimus*, AMNH 1347A (holotype). Bar scale = 1 cm.

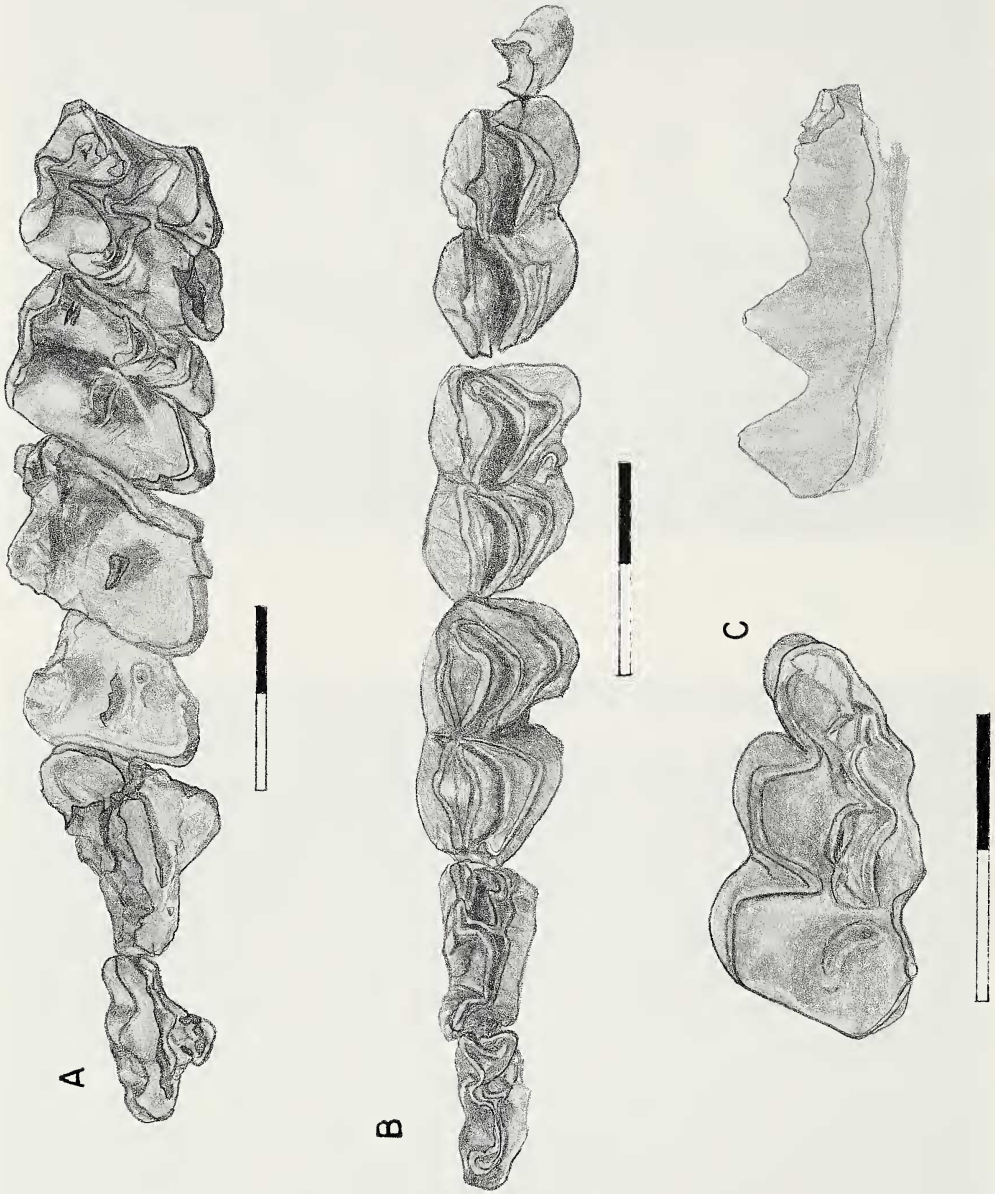


Fig. 12.—Cheek teeth of *Leptomeryx obliquidens*. A. P²-M³, YPM 10541 (holotype). B. P₃-M₃, YPM 2248. C. Occlusal view (left) and lingual view M₃, YPM 10541 (holotype). Bar scale below each figure = 1 cm.

obliquidens and *L. minimus* (?=*L. exilis*). The other lineage includes the Chadronian *L. speciosus*, Orellan *L. elissae* and *L. evansi*, the Whitneyan *L. lenis* (?=*L. evansi*) and additional species similar to *L. evansi*, and possibly the Arikarean *L. agatensis*.

The only consistent character that separates these two groups throughout their known record is the morphology of the entoconulid on M_3 . The *L. yoderi*–*L. mammifer*–*L. exilis*–*L. obliquidens* lineage is characterized by a conical entoconulid that is triangular in lingual view, and is lower than the hypoconulid and strongly connected to it. In the *L. speciosus*–*L. evansi*–*L. elissae* lineage, the entoconulid on M_3 is cylindrical, equal in height to the hypoconulid, and separated from it by a deep, distinct valley (see Heaton and Emry, 1996:fig. 9).

In the first lineage, there is little morphological change through time except in size. There is increase in size during the Chadronian, from *L. yoderi* to *L. mammifer*, then a marked reduction in size at the Orellan boundary with *L. exilis* which persists into the Whitneyan (?=*L. minimus*). Also in the Whitneyan there is a marked increase in size with the appearance of *L. obliquidens*. The latter also shows the first change in morphology with the crenulation of the enamel on the cheek teeth.

The *L. speciosus*–*L. evansi*–*L. elissae* lineage shows an increase in the occurrence of the *Palaeomeryx*-fold on the lower molars and increased crenulations on the cheek teeth from *L. speciosus* to the Orellan *L. evansi* along with a reduction in size. However, the second Orellan species, *L. elissae*, lacks these derived features of *L. evansi*, and is nearly identical to *L. speciosus* except for its smaller size (even smaller than *L. evansi*). The Whitneyan and later species of this group appear closely related to *L. evansi* with the presence of the *Palaeomeryx*-fold and crenulations on the cheek teeth.

The only Arikarean or later leptomerycids that may have been derived from either of these lineages is *Pronodens*. The latter has slightly higher crowned cheek teeth than *Leptomeryx* and a reduction and modification of the anterior dentition (Taylor and Webb, 1976; Webb, 1998). However, the *Palaeomeryx*-fold is more prominent than in *L. evansi* and the entoconulid has the S/E-type of morphology of the *L. evansi* lineage as well. It is likely that *L. evansi* or a similar species in that lineage was directly ancestral to *Pronodens*.

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APPENDIX I

Referred specimens of Orellan *Leptomeryx evansi* examined in this study.

Nebraska (unspecified level in Orella Member)

CM 175 (3 specimens), 185 (2 specimens), 205 (3 specimens), 226 (5 specimens), 362, 442 (3 specimens), 455 (2 specimens), 472, 458, 2497, 3674 (2 specimens), 3679, 3680 (4 specimens), AMNH 53572 (2 specimens), 53573 (9 specimens), 53621, 53627 (3 specimens), 53626 (3 specimens), 330-726, 330-729, 546-24643, 570-24857, 602-25441, 602-25485, 606-25836, 606-25861, 606-25869, 606-25874, 606-25879, 606-25882, 606-25937, 606-25946 (3 specimens), 611-26636, 611-26638, 611-26642, 611-26653, 611-26658, 611-26670, 611-26676, 611-26677, 616-27214 [Lower dental elements], CM 205 (7 specimens), 226 (6 specimens), 542, 2497, 3670, 3678, 3682, 3683, 3674 (2 specimens), 3675 (2 specimens), 3676, 3824, 9143, 9144, 9148, 9689 [Upper dental element].

Orella A (Nebraska)

UNSM 119625 through 119630, and 119641 through 119648 [Lower dental elements], UNSM 119649 through 119660 [Upper dental elements].

Orella C (Nebraska)

UNSM 119634 and 119661 through 119677 [Lower dental elements], UNSM 119678 through 119698 [Upper dental elements].

Orella D (Nebraska)

UNSM 119699 through 119706 and 119712, 119713 [Lower dental elements]. UNSM 119714 through 119726 [Upper dental elements].

North Dakota

CM 2010a, 28800, 28803a; USNM 78-5, 78-8, 78-22 [Lower dental elements]. CM 2010, 28645 [Upper dental elements].

South Dakota

USNM 9426c (holotype).

Wyoming

AMNH 0-75-1525, 0-81-1611, 0-94-1883, 0-120-2228, 0-442-2044, 058-1379, 088-1691a, 088-1699 [Lower dental elements].

APPENDIX 2

Referred specimens of Orellan *Leptomeryx exilis* examined in this study.

Nebraska (unspecified level in Orella Member)

CM 1289, 73403, 73405, 73407, 73411, 73415, 73419, 73420, 73421; AMNH 53572 (2 specimens), 042-973q, 540-24592a, 606-25946 (3 specimens), 606-25875, 611-26678, 615-27163, 616-27220, 616-27252 [Lower dental elements]. CM 73412 [Upper dental element].

Orella A (Nebraska)

UNSM 119617, 119631, 119632 [Lower dental elements]. UNSM 119621 [Upper dental elements].

Orella C (Nebraska)

UNSM 119600 through 119615, 119618 through 119620, and 119633 [Lower dental elements]. UNSM 119623, 119624 [Upper dental elements].

Orella D (Nebraska)

UNSM 119616 [Lower dental element]. UNSM 119622 [Upper dental element].

South Dakota

AMNH 38838a, 90281, 208-3596-3, 208-3596-7, 230-4183, 230-4276, 230-4277 [Lower dental elements]. CM 9121; AMNH 25858, 53582a, 53596, 606-25840, 606-25857, 611-26647 [Upper dental elements].

Colorado

AMNH 6652, 6664, 9002 [Lower dental elements].

Wyoming

AMNH 0-142-2983g [Lower dental element].